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Spurs and ornaments among *Polyplectron* (Phasianidae)

by G. W. H. Davison

The generic name *Polyplectron* means ''many spurred'', and spur numbers greater than one per leg have been recorded in all 6 pheasants of the genus. This paper describes the variations in armature within and between species, and their relationship to age, body size and plumage extravagance.

Only males have spurs: they are sharp, slightly curved, with a bony core and keratinous sheath, and arise from the rear face of the tarsus. Two spurs on a leg are usually well separated, but a third and a fourth grow by doubling of the others (Davison 1985).

Spurs in *Polyplectron* are presumably important in intrasexual fighting (Geist 1977), as described for the Malaysian Peacock Pheasant *P. malacense*, the only species whose behaviour in the wild is known to any extent (Davison 1983a, 1983b). In this species, and apparently 3 others for which there is circumstantial evidence from the wild (Ogilvie-Grant 1897, Smythies 1953) or captivity (Stapel 1976), territory holding males clean the display sites to which females are attracted by their calls. The number of males so behaving varies widely from year to year.

If males with more spurs are more likely to win fights for territories and thus to breed, spur number would become an important factor in sexual selection. Such a case would be most unusual in that the weaponry used in intrasexual competition among males is distinct from the ornaments — in this genus iridescent eye-spots — of potential significance in non-combative assessment of phenotypic quality. Studies in this group thus hold interesting prospects for partitioning variance in reproductive success into components associated with male-male competition and with female choice.

Two initial assumptions are made here: first that the selective advantage of possessing more spurs does not arise through use of spur number as a visual cue to assess the rank or fighting ability of rivals. Visual assessment seems unlikely because spurs are in an inconspicuous position, are inconspicuously coloured, and no spur-revealing display is known; and second that males with many spurs will with the same effort inflict greater damage on their opponents than males with few spurs, though this does not imply that males with more spurs are necessarily stronger or have better fighting techniques.

Materials and Methods

Skins of males of all 6 species in the genus were examined, from the British Museum (Natural History) (105), the Zoological Reference Collection, National University of Singapore (18), Cambridge University Museum of Zoology (6) and the Department of Zoology, University of Malaya (3), as well as 20 live males in various zoological gardens. Further data were most kindly supplied by curators at the American Museum of Natural History (51), Rijksmuseum van Natuurlijkehistorie (27), Field Museum of Natural History (26), United States National Museum (12) and Merseyside County Museum (2). Spur number was counted on each skin or live bird, and expressed as the total number of spurs per male. Some captives were observed throughout adolescence and for up to 10 years of adulthood, to record any changes in spur number.

Wing-length was measured as the chord from carpal to tip of the longest primary, tail-length as distance from the point of insertion to tip of the longest rectrix. Wing-length was assumed to be directly related to body size. Relative tail-length was taken as tail-length divided by wing-length. For the 132 skins examined personally the length of each spur was taken as the chord from tip to basal scales. Three age categories were distinguished: juveniles, in which the dorsal plumage lacked any adult-like feather; adolescents, with from one to all except one dorsal feather adult-like; and adults, with no juvenile dorsal feathers remaining. Adolescent *P. bicalcaratum* and *P. malacense* were further subdivided into those with less than or with more than half the dorsum adult-like.

Males of most species bear iridescent ocelli on the wings and tail. Where present, the maximum (a) and minimum (b) radii of the largest such ocellus on the secondaries and on the rectrices were measured, and used to calculate their iridescent surface areas (A) using the formula $A=\pi ab$. The separate and combined surface areas of these 2 largest ocelli were used as indices of plumage extravagance. The technique is approximate, and can be faulted because the ocelli are not perfect ellipses, in some species having blurred edges, and they are hard to measure on damaged or distorted feathers. Ocelli were measured only on those skins examined personally.

Problems with the use of museum material, with possible bias towards easily collected birds, are discussed in a section on confounding factors.

Results

Results on spur number for each species and age class are summarized in Table 1. Several small juveniles lacked any trace of spurs. These were regarded as sufficiently young that spur growth had not yet begun; they are bracketed in the Table and were ignored in the calculation of mean spur number.

Spur number was not distributed normally, showing for *P. bicalcaratum* a slight negative skew ($a_3 = -1.99$, $p < 0.10$).

Spur number versus age

Mean spur number did not differ significantly between age classes for any species (Kolmogorov-Smirnov 2-tailed tests, $p < 0.20$). The lack of significant correlation between spur number and age could have been due to the small sample size of young males, but data from captives indicate that spur number is fixed in the individual.

One adult male *P. malacense* possessed 4 spurs from the beginning of observations in December 1974 until at least November 1984. Two male

TABLE 1

Distribution of spur number among different age groups of *Polyplectron* species.
Numbers of small juveniles are bracketed

	Age (n)	Number of spurs								Mean no.
		0	1	2	3	4	5	6	7	
P. chalcurum	Adult (39)	1	1	4	4	26	3	−	−	3.59
	Juvenile (9)	(1)	−	1	4	3	−	−	−	3.25
P. inopinatum	Adult (11)	−	−	2	3	5	1	−	−	3.45
	Juvenile (1)	(1)	−	−	−	−	−	−	−	−
P. germaini	Adult (12)	−	1	−	−	8	3	−	−	4.00
P. bicalcaratum	Adult (85)	2	2	4	6	58	10	2	1	3.87
	Adolescent (7)	−	−	1	1	5	−	−	−	3.57
	Juvenile (4)	(1)	−	−	−	3	−	−	−	4.00
P. malacense	Adult (27)	−	−	−	2	20	4	1	−	4.15
	Adolescent (12)	−	−	−	1	9	1	1	−	4.17
	Juvenile (9)	(1)	−	−	3	5	−	−	−	3.63
P. emphanum	Adult (42)	−	1	1	2	37	1	−	−	3.86
	Adolescent (6)	−	−	1	−	4	1	−	−	3.83
	Juvenile (6)	(2)	1	−	1	2	−	−	−	3.50
	TOTALS	3(6)	6	14	27	185	24	4	1	

P. emphanum were already spurred at adolescence at age 12 months and in neither case, one with 3 spurs and the other with 4, did spur number change by the age 5 years. Another male *P. emphanum* developed no spurs at adolescence and still had none by age 2 years. Though all spurs may not erupt quite simultaneously in the young bird, spur number evidently does not increase after adolescence.

Spur number versus species

The greatest observed range in spur number, 0-7 spurs, was in *P. bicalcaratum,* for which the sample size was largest. Species differences in mean spur number did not approach significance when compared within or even across age classes (Kolmogorov-Smirnov 2-tailed tests, $p > 0.20$). For each species the mode was 4 spurs, 2 per leg. The 2 small long-tailed species, *P. chalcurum* and *P. inopinatum,* for which there is no record of defended fixed display sites, did not differ from the remaining species in spur number.

Spur length versus age

Table 2 compares the mean lengths of spurs between age classes for 3 species with large sample sizes. Clearly spurs grew as males matured. For *P. malacense* and *P. emphanum* spurs averaged longest in late adolescence, although for each species the single longest spur was in an adult. A slight decline after reaching adulthood might be attributed to wear, whether or not spurs then cease to grow.

Although subject to severe constraints of sample size, Table 2 hints that the peak phase of spur growth in *P. malacense* may occur earlier relative to plumage changes than in *P. bicalcaratum.* In *P. bicalcaratum* the biggest jump in spur length occurred between late adolescence and adulthood, whereas in *malacense* it occurred between the juvenile and early adolescent samples. In *P. emphanum* spurs were substantially developed even in 2 juveniles examined.

One interesting incidental was the proportion in the sample measured of males not yet in adult plumage: 44% for *P. malacense* and 21% for

TABLE 2

Mean spur length according to age class in males of 3 *Polyplectron* species

	Juvenile	Early adolescent	Late adolescent	Adult
P. bicalcaratum				
Number of birds	3	1	1	27
Number of spurs	12	4	4	102
Mean spur length, mm	2.36	2.25	3.25	8.86
SD	1.53	1.03	2.51	1.48
P. malacense				
Number of birds	8	6	6	22
Number of spurs	29	26	24	90
Mean spur length, mm	3.69	8.72	11.58	10.28
SD	2.29	4.09	2.30	2.26
P. emphanum				
Number of birds	2	3		9
Number of spurs	7	12		35
Mean spur length, mm	7.07	11.19		10.53
SD	1.50	0.87		1.06

P. emphanum, yet only 11% for *P. bicalcaratum.* Whether this is important, and the possible role of biassed capture techniques, is discussed later.

Spur number versus size

For each species Spearman Rank correlations, r_s, were calculated for pairs of morphological criteria (Table 3).

In 5 out of 7 taxa, greater wing length was significantly correlated with greater tail length and higher spur number. High spur number was correlated with greater tail length in 4 taxa and with greater tail to wing ratio in 3. There were few significant correlations between ocellus areas and other measurements.

Amongst the 7 taxa in Table 3, the number of significant correlations was highly related to sample size ($r_s=0.8571$, $p<0.01$); 85% of correlations were significant for the 20 samples containing 30 birds or more, but only 20% were significant for the remaining smaller samples. Thus the correlations involving

TABLE 3

Spearman Rank values for various plumage and spur correlations among *Polyplectron* species. Significant correlations are marked * ($p<0.05$), ** ($p<0.01$) or *** ($p<0.001$), and sample sizes are given in parentheses.

			P. chalcurum	*P. inopinatum*	*P. b. bicalcaratum*	*P. b. bakeri*	*P. b. ghigii*	*P. malacense*	*P. emphanum*
Wing length	v	Tail length	0.671*** (35)	0.300 (11)	0.636*** (34)	0.505** (30)	0.236 (13)	0.527* (18)	0.540*** (39)
Wing length	v	Spur number	0.479** (35)	0.280 (12)	0.392* (34)	0.496** (30)	0.173 (13)	0.514* (18)	0.497*** (39)
Spur number	v	Tail length	0.405* (35)	0.239 (11)	0.576*** (34)	0.323* (30)	0.150 (13)	0.384 (17)	0.490** (39)
Spur number	v	Tail: wing ratio	0.412** (35)	0.293 (11)	0.548*** (34)	0.305 (30)	0.345 (13)	0.218 (17)	0.508*** (39)
Wing length	v	Tail: wing ratio	0.514** (35)	−	0.344* (34)	0.305 (30)	−0.124 (13)	−0.140 (17)	0.202 (38)
Wing length	v	Wing ocellus area	−	0.821** (8)	0.687** (17)	−0.047 (18)	0.013 (9)	0.366 (17)	−
Tail length	v	Tail ocellus area	−	−0.300 (5)	0.074 (17)	0.307 (18)	−0.317 (9)	0.485* (16)	−0.196 (7)
Wing length	v	Total ocellus area	−	−	0.429* (17)	0.106 (18)	−0.158 (9)	0.382 (16)	0.384 (7)
Spur number	v	Total ocellus area	−	−	−0.054 (17)	0.693*** (18)	0.475 (9)	0.337 (16)	0.313 (7)

TABLE 4

Means of morphological criteria for male *Polyplectron malacense,* ranked according to spur number. Wing and tail measurements in mm, ocellus areas in mm^2.

	n	Spur no.	Wing	Tail	Tail/Wing	Largest wing ocellus	Largest tail ocellus	Combined ocellus area
P. malacense adolescents	1	3	208	175	0.84	170	217	387
	8	4	203	200	0.98	143	372	515
	1	5	212	225	1.06	–	319	–
	1	6	215	240	1.12	112	418	530
P. malacense adults	1	3	210	209	1.00	159	377	536
	15	4	214	225	1.06	190	423	613
	4	5	223	229	1.03	193	437	630

ocellus areas, statistically real only in one taxon and all based on samples of fewer than 20 birds, deserve reinterpretation if additional measurements become available. At least for one other species, *P. malacense,* mean ocellus areas appear to rise with spur number (Table 4).

Scattergrams (Figs. 1 and 2) show that the correlation between size and spur number is based on a deficiency of large, few-spurred males. Many-spurred males (3-5 spurs) show a broad range in wing and tail lengths, but few-spurred males are always small.

Confounding factors

All wing, tail and ocellus measurements were taken from museum skins. Use of museum samples carries an obvious risk of bias towards easily caught
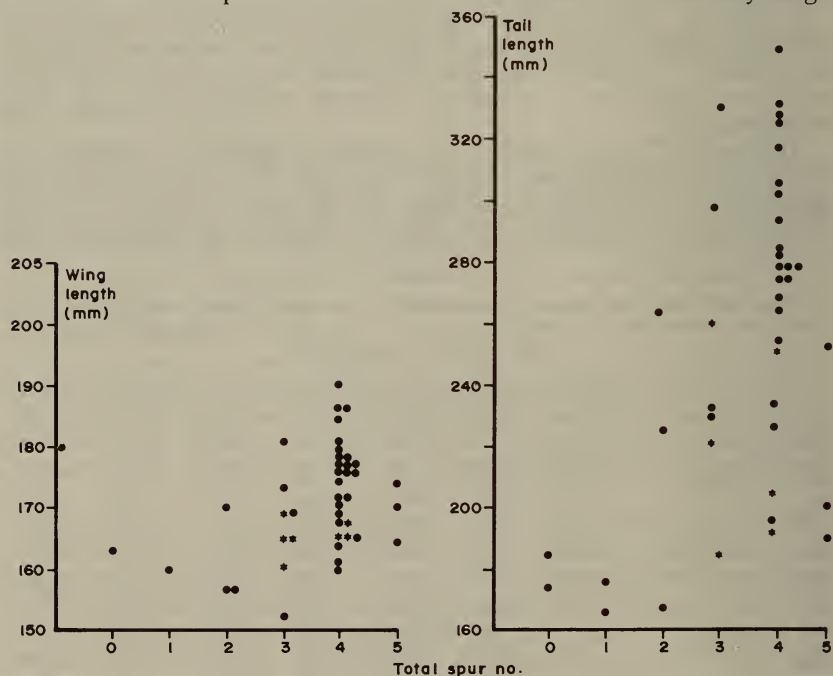

Figure 1. Scattergram of wing and tail length according to spur number in adults (spots) and juvenile (stars) of male *Polyplectron chalcurum.* Two 4-spurred adults with very long tails (387 mm, 401 mm) are not shown.
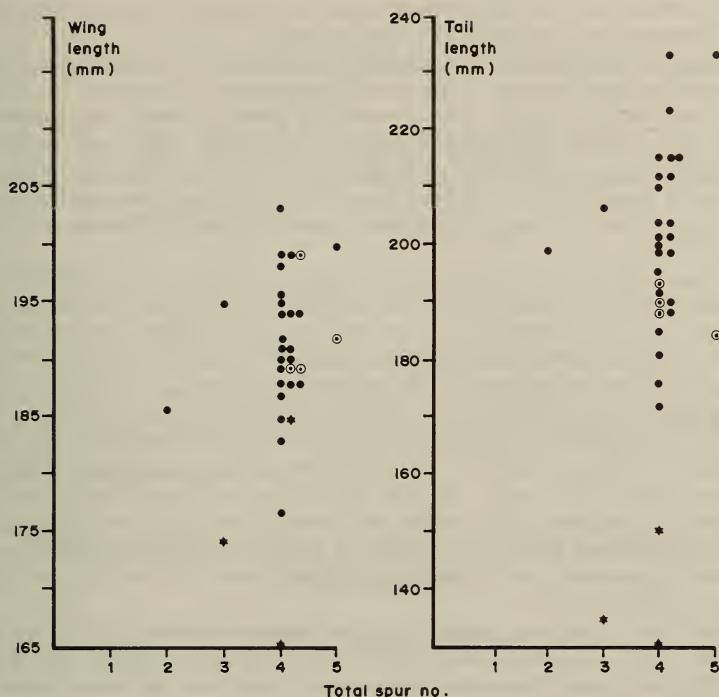
Figure 2. Scattergram of wing and tail length according to spur number in male *P. emphanum*. Filled circles represent adults, circles adolescents, and stars juveniles.

males; for instance, many-spurred noisy territorial males might attract a collector's attention. First, however, this would not explain the drop in total of 5- to 7-spurred males. Second, the distribution of spur number is similar in every species whether subadults, presumably non-territorial (Davison 1983a), are few or many. Third, most of the *P. chalcurum* skins examined are known to have been collected by ground snare (Robinson & Kloss 1918, 1924), a method presumably not biassed towards conspicuous birds. In short, the heavy representation of 4-spurred males in all species is likely to be a real phenomenon, while the correlations between spur number and size are not influenced by sampling technique.

Discussion

Beyond that point when spurs first erupt in the juvenile, spur number is not related to further age changes. It might be heritable or be influenced by nutrition of the chick prior to spur eruption. It might reflect absolute weight achieved by the time of adolescence, through food quality, nutrient balance, rate of calcium deposition as bone, and so on.

Of the above possibilities genetic determination of spur number seems likely because this has been demonstrated in related birds. In domestic fowl *Gallus domesticus* the possession of a second spur per leg is heritable (Washburn & Smyth 1971). Warren (1946) considered possession of supernumerary spurs in

fowl to be recessive, and Hutt (1941) found that recessive homozygotes of the breed Sumatra Fowl had up to 5 spurs per leg.

Multiple spurs have also been reported in wild turkeys *Meleagris gallopavo,* their marked geographical restriction suggesting a mutation in a local population (Williams 1967). The presence or absence of spurs in female wild turkeys also follows geographical patterns consistent with local mutations (Williams & Austin 1969, Pattee & Beasom 1977). The presence or absence of spurs in female White Leghorn fowl is genetically determined (Goodale 1925) and is not influenced by dietary manipulation (Christmas & Harms 1982).

Spur number in *Polyplectron* is related to size. Size is presumably both heritable (Boag & Grant 1978, Moss & Watson 1982) and related to early nutrition, but in addition large males with few spurs might rapidly be beaten, and die. They could be compared with adopters of an unsuccessful ''bluff'' strategy (Rohwer & Rohwer 1978), whose large size and plumage features imply a dominance which they are unable to enforce because of their low spur number. Alternatively, increasing spur number might be related to increasing potential for body growth beyond adolescence, only males with high spur numbers having the capacity to grow big. There are theoretical grounds for expecting size increase over the first few breeding seasons in sexually selected species (Andersson 1982), and there is empirical evidence of this in the pheasant *Argusianus argus,* in which the oldest known bird was also the largest (Delacour 1977).

Polyplectron is the only multiple-spurred genus which is not monogamous (Davison 1985). If the number of spurs is genetically determined, as in related birds, then only some males could achieve high spur number even if spurs are individually cheap to produce. Yet the maintenance of variation within populations suggests there may be conflicting advantages to low versus high spur number. Variation in size and spur number, and in proportions of adolescent plumaged males, might open the way to alternative reproductive strategies. Field observations should make this clear.

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Relationships of the Pacific warbler *Cichlornis* and its allies

by S. Dillon Ripley

Recently Hadden (1983) described a new species of thicket-warbler of the genus *Cichlornis* from Bougainville Island, North Solomons Province, Papua New Guinea. This new taxon, *C. llaneae,* was based on a single unsexed study skin, mist-netted in the forested hills above the site of the Panguna Copper Mine. Subsequent to this remarkable discovery, additional specimens of the new bird have been procured, and additional new information on its biology has been assembled, based on the results of a field trip to Bougainville Island sponsored by the Smithsonian Institution. Here I report these new findings, and comment on the relationship of this new taxon to other thicket-warblers and on their relationships to other Pacific warbler genera.

Bruce Beehler visited Bougainville Island 11-19 June 1980 in order to conduct a brief avifaunal survey of the montane forest where Hadden had discovered the thicket-warbler, and by mist-netting to obtain for the Smithsonian a series of montane forest birds endemic to Bougainville, especially additional representatives of the new thicket-warbler. Hadden gave generous assistance and in addition visited the collecting camp for 3 days while Beehler was there.

During this trip 2 specimens of the new *Cichlornis* were taken, sexed and prepared as study skins, one of the birds being trapped while brooding 2 eggs on a nest. These 2 specimens are of great value because they provide information on sexual dimorphism, adult plumage, weight, rectrix shape, tail length, and soft part coloration, hitherto unavailable for the Bougainville population. These data appear in Table 1 along with information from the holotype of *llaneae.*